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Courtship and Copulation in Glaucous-Winged Gulls, Larus Glaucescens

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ABSTRACT

COURTSHIP AND COPULATION IN GLAUCOUS-WINGED GULLS, *LARUS GLAUCESCENS*

by

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ABSTRACT OF GRADUATE STUDENT RESEARCH

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Title: COURTSHIP AND COPULATION IN GLAUCOUS-WINGED GULLS, *LARUS GLAUCESCENS*

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Using video recordings and scan counts, I examined the occurrence, sequences, and durations of behavior and environmental factors associated with courtship and copulation in glaucous-winged gulls, *Larus glaucescens*. Males and females in a pair had equivalent pre- and post-Mount behavior occurrences and durations. The main courtship sequence was Head Toss → Courtship Beg/Respond to Beg → Mounted/Mount, and females appeared to initiate transitions between these pre-Mount behaviors. More Mounts occurred during the egg-laying stage of the breeding season, but copulation duration, wing-flag duration, and cloacal contacts per copulation showed no significant differences across sampling periods. Poisson analysis showed no significant grouping of Mounts in time during the days sampled. Bald eagle (*Haliaeetus leucocephalus*) disturbance was

correlated with increased courtship and copulation frequency. Other environmental factors affecting courtship and copulation included day of year, tide height, and solar elevation. Peak Mounts and Courtship Begs per territory occurred two days before the peak Courtship Feeds and 10 days before peak clutch initiations.

Andrews University

College of Arts and Sciences

COURTSHIP AND COPULATION IN GLAUCOUS-WINGED GULLS, *LARUS GLAUCESCENS*

A Thesis

Presented in Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

Kelly M. McWilliams

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CHAPTER 1

INTRODUCTION

Copulation is directly involved in avian reproduction, and if behaviors preceding copulation influence copulation, they also could influence fitness. Moreover, environmental factors such as habitat, food supply, seasonal cycles, photoperiod, temperature, climate, predation, and interspecific social interactions affect the seasonal and daily timing of breeding, the cost of reproduction, and breeding success of birds (Gochfeld, 1980; Slagsvold, 1984; Price et al., 1988; Baird, 1990; Erikstad et al., 1998; Orzack & Tuljapurkar, 2001; Thomas et al., 2001; Good, 2002; Visser et al., 2004; Ball & Ketterson, 2008). Few studies, however, have examined copulation or precopulatory behaviors in relation to these environmental factors.

Larids are well suited for behavior studies; they are large, easily observed, and nest in the same large colonies year after year. Early research on larid reproduction focused on descriptions of courtship and copulatory behaviors, the temporal relation of these behaviors to the breeding season and daily environmental fluctuations (e.g., Moynihan, 1955, 1962; Tinbergen, 1959; Tinbergen, 1960; Vermeer, 1963; Brown, 1967; Burger, 1976) and on the social facilitation of courtship displays, copulation, and copulation synchrony (e.g., Hailman, 1964; Brown, 1967; Harris, 1970; Southern, 1974; Fetterolf & Dunham, 1985). A closer examination of individual reproductive behaviors, however, could expand our understanding of the role played by social facilitation and interaction during mating in larids.

The breeding biology of glaucous-winged gulls (*Larus glaucescens*) has been well-characterized (Vermeer, 1963; Verbeek, 1986; Hayward & Verbeek, 2008). In south British Columbia, pairs start arriving in February and most by early April; some pairs form immediately after arrival. Single males advertise and court females on their territories up to early May. Courtship continues as pairs form, build nests, copulate, and lay eggs (Hayward & Verbeek, 2008). No previous studies, however, have investigated the effects of environmental factors on daily patterns of courtship and copulation in this species, nor have fine-scale aspects of courtship and copulation been described. I investigated daily and seasonal patterns of courtship and copulation during the pre-egg-laying, egg-laying, and incubation stages of the 2008 mating season of a large glaucous-winged gull colony. Using video recordings, I analyzed the sequence and durations of courtship behaviors leading up to copulation and attempted copulation. I also investigated daily patterns of courtship and copulation in relation to environmental factors, including bald eagle (*Haliaeetus leucocephalus*) disturbances.

CHAPTER 2

METHODS

Data Collection

Data for this study were collected at Protection Island National Wildlife Refuge (48º08' N, 122º55' W), Jefferson County, Washington, U.S.A. Violet Point, a gravel spit extending southeast, contains a breeding colony of more than 2400 nesting pairs of glaucous-winged gulls (Henson et al., 2007). Bihourly courtship behavior scans were collected as well as video recordings of a small section of the colony.

Courtship Behavior Scans

From 13 May to 22 June 2008, occupancy counts and behavior scans were made every 2 hrs from 0600-2000 hours Pacific Daylight Time (PDT). The scanned colony area was divided into five plots representing a variety of habitats, with a combined area of 4205 m^2. All observations were made using a 20-60x spotting scope from an observation point atop a 33 m bluff at the west end of Violet Point. During scans, any unusual circumstances such as deer or eagle disturbances, rain, extreme wind, etc., were noted. During disturbances, counting was halted while some or all the gulls in the area of the disturbance flew up and circled the colony (Hayward & Verbeek, 2008). Counts were resumed only after the birds settled to the ground, stopped alarm calling, and began preening and resting. Time, approximate location, and scope of the disturbance were noted. Clutch initiation, indicated by the first egg laid, was recorded daily by nest inspection from 13 May to 22 June 2008. A weather station located 2 m above site elevation on the northwest end of Violet Point recorded hourly values of several environmental conditions on the colony, including relative humidity, temperature, wind speed on the colony, and barometric pressure. I obtained hourly solar elevations and tide heights from the National Oceanic and Atmospheric Administration (NOAA), Port Townsend Station, ID 9444900 (http://co-ops.nos.noaa.gov/), corrected by 0.93 to account for a small difference in tide height at Protection Island.

Courtship, Mounting, and Copulation Behavior Descriptions

During behavior scans, the incidences of four behaviors were recorded: Paired Head Toss, Courtship Beg/Respond to Beg, Courtship Feed, and Mount. If a pair transitioned from one behavior to another of these four behaviors during the 10 min scan, it was recorded as a new behavior instance. During Head Toss, the head and bill flip upward suddenly; this movement is repeated at short intervals and is accompanied by the Head Toss Call (Hayward & Verbeek, 2008). In Paired Head Toss, both members of the pair engaged in the behavior. Courtship Beg consists of female Head Toss with the female located in front of male and touching or tugging at his bill (‘Pulling’; Brown, 1967). Male Response to Beg involves sporadic Head Toss by the male in response to female Courtship Beg. Response to Beg could be followed by Courtship Feed, during which the male regurgitates food either into female’s bill or onto the ground in response to Courtship Beg. Courtship Beg also could be followed by the male mounting the female, referred to as Mount. Just prior to Mount, the male begins the Copulation Call, stretches his neck, and opens his wings. Once in Mount, the male beats his wings (‘wing flagging'; Southern, 1974), continues the Copulation Call, and wags his tail side-to-side prior to each cloacal contact. During Mount, the female Head Tosses and tugs at the male's breast feathers and bill. After a Mount, both birds may preen or bathe (Hayward & Verbeek, 2008).

Video Data Collection

During the 2008 breeding season, digital video recordings were made using a Sony HDR-SR12 120GB High Definition Handycam® Camcorder. The camcorder was housed in a blind at the edge of the colony and focused on a sample area that contained approximately 34 territories. Recordings were made from 0500-0800 and 1800-2000 PDT daily during the mating season; I analyzed 49 pre-Mount behavior sequences from the pre-egg-laying stage recorded on 23 May, 58 sequences from the egg-laying stage recorded on 6 June, and 40 sequences in the incubation stage of the breeding season recorded 21 June–23 June, involving a total of 30 hours of observation. For a given courtship bout, I recorded all behaviors following the first courtship behavior preceding a Mount, and the sequence and duration (in 1-sec units) of each subsequent behavior. Behaviors were considered continuous if they were not interrupted for more than 1 sec by maintenance or resting behavior.

Several additional courtship behaviors were recorded during video observation, including Long Call, Courtship Mew, and Choke. During Long Call, the head swings down between the legs until the bill points posteriorly (the Bow), at which time the bird starts to Long Call; the head then sweeps forward and upward (Hayward & Verbeek, 2008). Courtship Mew consists of one or both birds in the pair standing or walking with the neck arched, the head angled slightly downward, and emitting Courtship Mew Call

(Hayward & Verbeek, 2008). During Choke, one or both members of the pair crouch close to the ground with the bill pointed downward, tail pointed upward, breast heaving, emitting the Choking Call (Hayward & Verbeek, 2008). Allopreen also is considered a courtship behavior (Hayward & Verbeek, 2008), but it was not observed in this study. Other behaviors commonly observed during courtship bouts were Stand Intermediate, a standing posture with the neck halfway extended, and Walk.

Only courtship bouts that culminated in Mounts or attempted Mounts were included in the analysis. For each Mount, I recorded the duration from the time the male's feet contacted the female's back to the time his feet contacted the ground after dismounting. I also recorded the duration of male wing flagging during Mount, taken to be continuous from Mount initiation if not interrupted by at least a 3-sec pause. Finally, I recorded the number of cloacal contacts during Mount; if this number was greater than zero, the Mount was considered a successful copulation. For each stage in the breeding season, I noted the number of sequential Mounts by pairs (during which a pair engaged in successive Mounts following one main bout of courtship) and the number of multiple Mounts (Mounts from the same pairs during a 3-hr recording). After Mount, I recorded subsequent behaviors until both members of the pair were preening or in a rest posture, one or both birds exited the territory, or until 1 min elapsed. For a given 3-hr video sample, data for each behavior bout surrounding a Mount were from different pairs.

Analysis of Video Data

For each stage of the mating season, I recorded the initiating courtship behaviors and the occurrence (whether each behavior occurred or did not occur during each courtship bout) and percent occurrence (the total number of incidences in relation to the total number of sequences analyzed during that stage of the season) of each behavior. A courtship bout included all events from the first courtship behavior to the beginning of the first Mount. I compared the number of occurrences between males and females using the chi-squared test, assuming an equal distribution of occurrence of each behavior by males and females. To compare sequences of courtship behaviors at the three stages of the breeding season, I determined the five most commonly occurring behaviors by males and females preceding Mount. For males and females separately, I compared the incidence of all behaviors before and after the five most common behaviors in relation to one another. Behaviors in addition to the five most common behaviors were lumped into a category designated as 'Other.' I also determined the two most common female behaviors following and the most common behavior occurring during each common male behavior, and vise versa, as a means of characterizing common behavior sequences.

I compared the number of first Mounts during the morning and the evening to expected values; expected values were generated by assuming an equal distribution of Mounts during the morning and evening within each stage of the season. I compared the total number of Mounts during each stage sampled to expected values that were based on the number of hours sampled during each stage (6, 6, and 18 hrs for the pre-egg-laying, egg-laying, and incubation stages, respectively). For each stage, I compared the number of successful Mounts to expected values based on the proportion of total Mounts observed during each stage. I also compared the average successful single Mount durations with a one-way ANOVA, and wing-flagging durations and number of cloacal contacts per copulation among the three stages using the Kruskal-Wallis test. I excluded all instances of sequential Mounts. To evaluate whether the incidence of Mount was clustered in time, I used the chi-square test to compare first Mount distribution during 5-min intervals to a Poisson distribution. Only first Mounts were counted if pairs engaged in sequential Mounts, but two or more Mounts by a pair were counted if separated by intervals of non-reproductive behavior. Following the first Mount, I tallied the occurrence and percent occurrence of the six most commonly occurring behaviors as well as any courtship behaviors (only Head Toss and Choke occurred after the first Mount) and further multiple Mount attempts. I also determined the percentage of bouts during which Head Toss occurred (bouts with sequential Mount attempts were excluded).

For the five most common courtship behaviors, plus Choke and Long Call, I determined the total time spent by each bird of a pair engaging in each behavior before the first Mount. After first Mount, I determined durations of the most commonly occurring male and female behaviors plus Head Toss. For each bout I calculated the proportion of time occupied by each male and each female pre-Mount and post-Mount behavior in relation to each of the pre-Mount or post-Mount durations, respectively. I compared these proportions by reproductive stage using a Kruskal-Wallis test.

Effects of Environmental Conditions

I used logistic regression to investigate the effects of environmental conditions on the incidence of three focal behaviors in the scan data: Paired Head Toss, Courtship Beg, and Mount. To estimate the number of established territories with pairs available to engage in the focal behaviors for each day of data collection, I used the number of birds present in the five plots during each day's last occupancy count divided by 2, fit a curve to those daily values, and estimated the daily established territories from the curve. I assumed that the three focal behaviors did not occur outside of the observed plots. For

Mount, I examined the effects of six factors: day of the year, ambient temperature, wind speed, solar elevation, tide height, and occurrence/nonoccurrence of an eagle disturbance during the scan. For Head Toss, I examined the effects of the day of year, wind speed, solar elevation, tide height, and eagle disturbance. For Courtship Beg, I examined the effects of the day of year, temperature, solar elevation, tide height, and eagle disturbance.

The probability that a pair was involved in a particular behavior, given a set of environmental factors x, is denoted $\pi(x)$. Logistic regression models the probability $\pi(x)$ by regressing the log-odds, or 'logit'

$$g(x) = \ln\left(\frac{\pi(x)}{1-\pi(x)}\right)$$

on the environmental factors *x*. I inspected scatter plots of the logit of the observed frequencies against each environmental factor to verify that the logit was a roughly linear function of each factor. For Mount and Courtship Beg, the logit was nonlinear with respect to the day of year, so I transformed the day of year to make the effect linear. To do this, I found the peak day of Mount and Courtship Beg and replaced 'day of year' by the number of days away from the peak day. All other factors produced roughly linear trends. For each of the three models, I used the generalized linear regression function 'glmfit' in the Statistics Toolbox in MATLAB® (The MathWorks™, 2005). I suspected some overdispersion due to a lack of independence in individual responses. MATLAB adjusts for this by estimating a variance inflation factor and adjusting standard errors, confidence intervals, and p-values accordingly.

If an event occurs with probability π, then the 'odds' are $\pi/(1-\pi)$; in the context of logistic regression, the 'log-odds' are given by the logit $\ln(\pi(x)/1-\pi(x))$. The log of the ‘odds ratio’ (OR) for outcomes occurring under any two different conditions (two different environmental covariates) x_1 and x_2 is

$$\begin{aligned}\ln(OR) &= \ln\left(\frac{\pi(x_1)/1-\pi(x_1)}{\pi(x_2)/1-\pi(x_2)}\right)\\ &= \ln\left(\pi(x_1)/(1-\pi(x_1))\right)-\ln\left(\pi(x_2)/(1-\pi(x_2))\right)\\ &= g(x_1)-g(x_2)\end{aligned}$$

where g is the logit function. The OR is therefore

$$OR = e^{g(x_1)-g(x_2)}.$$

If factor x (with coefficient β) increases by c units, from x to $x + c$, while all other factors remain constant, then the odds ratio

$$OR = \exp\big(g(x+c)-g(x)\big) = \exp(c\beta)$$

is a measure of the effect of this increase on the system. OR > 1 indicates that the event is more likely than it was before, and OR < 1 indicates that the event is less likely (Hosmer & Lemeshow, 2000). The 95% confidence interval is given by

$$\exp\left[c(\beta \pm 1.96SE(\beta))\right]$$

where $SE(\beta)$ is the standard error estimation of β adjusted for overdispersion using the variance inflation factor.

All statistical tests were carried out at the $\alpha = 0.05$ significance level.

CHAPTER 3

RESULTS

Courtship Initiation and Behavior Occurrences

Of 147 observed courtship bouts during the breeding season, courtship was initiated by the male 53 times individually (when the female was not concurrently engaging in a courtship behavior) and by the female 55 times individually. Males and females initiated courtship simultaneously during 37 of the bouts (Table 1). During all simultaneously initiated courtship behaviors, the male and female engaged in the same behavior except in two instances: female Head Toss with male Mew, and female Mew with male Choke. To simplify reporting in Table 1, these two simultaneous initiation bouts were excluded, making the total observed initiations equal 145. Assuming an equal distribution of occurrence between males and females for each singly-initiated behavior, chi-square tests showed behavior occurrence was not significantly different for males and females for any observed behavior (Table 1).

For both males and females, the five most common behaviors occurring during courtship bouts before the first Mount were Head Toss, Beg/Respond to Beg, Stand Intermediate, Walk, and Mew, respectively. Males and females did not exhibit significantly different occurrences of observed courtship behaviors when compared with chi-square tests (Table 2). Expected values were generated by assuming an equal distribution between male and female occurrences. Of the observed courtship behaviors, Head Toss and Beg/Respond to Beg exhibited the highest occurrence. For both males and females, every courtship bout included at least one occurrence of Head Toss or Beg/Respond to Beg. In a comparison of male and female behavior occurrences by reproductive stage, only the occurrence of male Choke differed significantly from expected (pre-egg-laying n = 9, egg-laying n = 9, incubation n = 0; $\chi^2 = 6.91$, $df = 2$, p = 0.03; Table 10, Appendix). Expected values were generated by determining the proportion of the courtship bouts in each stage to that of the total, then multiplying that value by the total number of occurrences of each behavior for males and females separately.

Courtship Behavior Sequences

Figure 1 shows the most common pre-first-Mount sequences of behaviors for males and females. The two most frequent behaviors immediately following each of the five most common pre-Mount behaviors (Head Toss, Beg/Respond to Beg, Stand Intermediate, Walk, Mew) are displayed (Figure 1; Table 11 and Table 12, Appendix). The most probable courtship sequence for the male was Stand Intermediate → Head Toss → Respond to Beg → Mount; Mew, Walk, and Other were alternate beginnings to this sequence. The most probable sequence for the female was Other → Head Toss → Courtship Beg → Mounted; Mew, Walk, and Stand Intermediate were alternate beginnings to this sequence. Figure 2 shows that the most probable pre-Mount male and female behavior sequence was reciprocated Head Toss → Beg/Respond to Beg → Mounted/Mount, with Other and Mew at times interspersed at the beginning of the sequence (Table 13 and Table 14, Appendix). The most common male behavior following female Head Toss was Respond to Beg, so Figure 2 shows this transition by female Beg following female Head Toss, as the female had to Beg for the male to Respond to Beg.

Females initiated Head Toss more frequently than males, when comparing instances in which only one member of the pair began to Head Toss first (male n = 43, female n = 68, $\chi^2 = 5.63$, $df = 1$, $p = 0.02$). Males and females simultaneously began to Head Toss during 30 courtship bouts. During 6 of the bouts, pairs did not engage in Head Toss, but instead transitioned from Courtship Beg to Mount. Beg/Respond to Beg often was used in addition to Head Toss during courtship, not occurring in only 25 of 147 (14.5%) observed courtship sequences.

Mount and Copulation

Following courtship, pairs immediately progressed to Mount. The number of Mounts by stage was significantly different than expected ($\chi^2 = 72.9$, $df = 2$, $p < 0.0001$; Table 3). Expected values were based on the proportions of time sampled during the pre-egg-laying, egg-laying, and incubation stages (6, 6, and 18 hrs, respectively). Numbers of Mounts in the morning versus evening also differed significantly from expected for the pre-egg-laying ($\chi^2 = 6.75$, $df = 1$, $p = 0.009$) and incubation stages ($\chi^2 = 6.10$, $df = 1$, $p = 0.01$), but not for the egg-laying stage ($\chi^2 = 0.063$, $df = 1$, $p = 0.80$; Table 3); expected values were generated by assuming an equal distribution of Mount occurrence between morning and evening. Mounts/hr, calculated from the total number of first Mounts from different pairs observed during the recording time, consequently varied between morning and evening recordings during the pre-egg-laying and incubation stages, but they were relatively constant during the egg-laying stage. A pair during the egg-laying stage engaged in 3 multiple Mounts, the most recorded during any 3-hr interval. During the incubation stage, a pair engaged in the most sequential Mounts recorded, with a total of 2 following the first Mount.

The number of successful Mounts of the total observed (minus all sequential Mounts) was not significantly different among the three stages ($\chi^2 = 1.08$, *df =2*, *p* = 0.58; Table 3). Expected values were based on the proportion of each stage's Mounts (successful and unsuccessful) of the total number of single Mounts, excluding multiple Mounts from the same pairs (*n* = 135). Average Mount durations by reproductive stage did not differ significantly ($F_{2,103} = 1.21$, *p* = 0.30), nor did wing flag duration (H = 0.898, *df =2*, *p* = 0.64), or cloacal contacts per copulation (H = 3.34, *df =2*, *p* = 0.19; Table 3). Mounts were not significantly clustered in 5-min intervals during any reproductive stage (Table 4).

Post-First-Mount Behavior Occurrences

Of the behaviors following the first Mount, the male behavior with the highest occurrence was Stand Intermediate, followed by Walk, Stand Preen, Shake Head, Look at Feet, and Stand Upright. The female behavior with the highest occurrence was Stand Intermediate, followed by Walk, Stand Preen, Shake Head, Shake Wings, and Stand Upright (Table 5). Only the occurrence of Look at Feet and Shake Wings significantly differed from expected (Table 5). Male Head Toss occurred in 16.4% of post-Mount bouts; 62.5% of those Head Toss occurrences were not followed by further Mount attempts. Female Head Toss occurred in 24.0% of post-Mount bouts, with 77.1% of these occurrences having no subsequent Mount attempts. The male incidence for the above behaviors did not differ significantly from expected between the three stages of the breeding season, but the female occurrences of Look at Feet (pre-laying *n* = 0, egg-laying

n = 5, incubation n = 8; χ^2 = 9.90, df =2, p = 0.007), Shake Wings (pre-laying n = 5, egg-laying n = 23, incubation n = 19; χ^2 = 11.4, df =2, p = 0.003), and Stand Upright (pre-laying n = 17, egg-laying n = 16, incubation n = 3; χ^2 = 7.05, df =2, p = 0.03) were significantly different (Table 16, Appendix). Expected values were based on the proportion of post-first-Mount bouts observed in each stage of the total observed.

Pre- and Post-First-Mount Behavior Percent Durations

I found no significant differences in pre-Mount or post-Mount behavior percent durations among the pre-egg-laying, egg-laying, and incubation stages (Table 17, Appendix). Table 6 reports the mean duration percentages for the three stages of the breeding season combined. Because Head Toss also occurred after Mounts more frequently than the 10 occurrences of sequential Mounts, I compared pre-first-Mount and post-first-Mount Head Toss duration percentages. For males over all three stages of the breeding season, median duration percentages were 33.8% before the first Mount and 13.0% after the first Mount; the distributions in the two groups differed significantly (Mann-Whitney U = 977.5, n_1 = 133, n_2 = 27, p < 0.0001). The median female duration percentages were 32.4% before the first Mount and 10.6% after the first Mount; the distributions also differed significantly (Mann-Whitney U = 1112.0, n_1 = 136, n_2 = 33, p < 0.0001).

Environmental Effects on Courtship and Mount

Table 7 shows the results of regressing Mount on the day of the year, temperature, wind speed, solar elevation, tide height, and eagle disturbance. With all other factors held constant, the odds of Mount increased 25% for every 5 days closer to the peak Mount day

(day 158; 6 June; Figure 3), by 17% with at least 1 eagle disturbance during a 10-min scan, and by 22% with a 1-m increase in tide height. No conclusions could be drawn about the effects of temperature, wind speed, or solar elevation, as confidence intervals bracketed the value 1. Table 8 shows the results of regressing Paired Head Toss on the day of year, wind speed, solar elevation, tide height, and eagle disturbance, when both birds in a pair were concurrently Head Tossing. All other factors held constant, the odds of Paired Head Toss decreased by 10% with a 20-degree increase in solar elevation and increased by 13% with a 1-m increase in tide height. No conclusions could be drawn about the effects of the day of the year, wind speed, or eagle disturbance, as confidence intervals bracketed the value 1. Table 9 shows the results of regressing Courtship Beg/Respond to Beg on the day of the year, temperature, solar elevation, tide height, and eagle disturbance. All other factors held constant, the odds of Beg/Respond to Beg increased 47% for every 5 days closer to the peak Beg day (day 158; 6 June; Figure 3), 14% with a 20-degree increase in solar elevation, 15% with a 1-m increase in tide height, and by 29% with at least 1 eagle disturbance during a 10-min scan, and by. No conclusions could be drawn about the effects of temperature, as confidence intervals bracketed the value 1.

Courtship Feed did not occur frequently enough for analysis using logistic regression with the available data. Figure 3 plots daily per territory values of Courtship Feed and shows a marked increase toward day 160 (8 June 2008), the peak Courtship Feed day. This peak occurred 2 days after the peak Mount and Courtship Beg day (day 158; 6 June) and 8 days before the peak clutch initiation day (day 168; 16 June).

Table 1. Behaviors initiating courtship during the mating season

	Male individual initiation	Female individual initiation	p^a	Total individual initiations	Simultaneous initiation
Head Toss	36 (24.8%)	44 (30.3%)	0.37	80	23 (15.9%)
Beg/Resp. to Beg	0 (0.0%)	0 (0.0%)	1.00	0	6 (4.1%)
Mew	12 (8.3%)	5 (3.5%)	0.09	17	5 (3.5%)
Long Call	5 (3.5%)	6 (4.1%)	0.76	11	1 (0.7%)
Choke	0 (0.0%)	0 (0.0%)	1.00	0	2 (1.4%)
Total incidences	53 (36.6%)	55 (37.9%)	0.85	108	37 (25.5%)

[a] The results of chi-square tests with expected values that assume an equal distribution of occurrences between males and females; $df = 1$.

Table 2. Occurrences of common male and female behaviors during pre-first-Mount courtship

Behavior	Male occurrences	Female occurrences	p^a
First Mount	147 (100.0%)	147 (100.0%)	1.00
Head Toss	135 (91.8%)	138 (93.9%)	0.86
Beg/Respond to Beg	121 (82.3%)	121 (82.3%)	1.00
Stand Intermediate	69 (46.9%)	63 (42.9%)	0.60
Walk	61 (41.5%)	48 (32.7%)	0.21
Mew	47 (32.0%)	30 (20.4%)	0.053
Choke	19 (12.9%)	16 (10.9%)	0.61
Long Call	14 (9.5%)	12 (8.2%)	0.70
Courtship Feed	13 (8.8%)	12 (8.2%)	0.84

[a] The results of chi-square tests with expected values that assume an equal distribution of occurrences between males and females; $df = 1$.

Table 3. First Mount, multiple Mount, and sequential Mount incidence, and copulation incidence, mean duration, wing-flag duration, and cloacal contacts per copulation during three stages of the mating season

	Time of recording	# first Mounts[a]	Expected # first Mounts	First Mounts/hr	Total # first Mounts/ stage[b]	Expected first Mounts/ stage	Total first Mounts/hr	# multiple Mounts[c]	# sequential Mounts[d]
Pre-egg-laying stage	0500-0800	33	24	11.0	48	30.8	8.0	7	4
	1800-2100	15	24	5.0					
Egg-laying stage	0500-0800	33	32	11.0	64	30.8	10.7	16	5
	1800-2100	31	32	10.3					
Incubation stage	0500-0800	29	21	3.2	42	92.4	2.3	1	1
	1800-2100	13	21	1.4					

	Successful Mounts[e]	Expected # successful Mounts	Mean copulation duration (s)	Mean wing flag duration (s)	Mean # cloacal contacts/copulation
Pre-egg-laying stage	39/44 (88.6%)	34.2	70.1±22.8	53.9±23.2	2.7±1.4
Egg-laying stage	39/52 (75.0%)	41.4	79.0±26.8	56.0±25.2	3.4±1.9
Incubation stage	27/39 (69.2%)	30.3	76.2±27.5	53.5±18.5	3.3±1.3

[a] Pre-egg-laying stage $p = 0.009$; Egg-laying stage $p = 0.80$; Incubation stage $p = 0.01$.
[b] $p < 0.0001$.
[c] Subsequent Mounts from pairs already recorded.
[d] Number of Mounts occurring in close succession after a main bout of courtship and first Mount.
[e] A successful Mount had one or more cloacal contacts and was considered a copulation; values exclude sequential Mounts.

Table 4. Poisson analysis of first Mount distribution in 5-min increments for three stages of the mating season

	Pre-egg-laying stage		Egg-laying stage		Incubation stage	
Mounts/ 5 min	Observed	Expected	Observed	Expected	Observed	Expected
0	40	46.2	34	42.5	181	183.7
1	23	20.5	25	22.4	30	29.8
2	4	4.6	10	5.9	5	3.3
>3	5	2.3	3	3.2	0	0.0
	$\chi^2 = 4.40$ $p = 0.22$		$\chi^2 = 4.82$ $p = 0.19$		$\chi^2 = 0.95$ $p = 0.81$	

Table 5. Occurrences of common behaviors following courtship and first Mount (*n* = 146 post-Mount bouts)

Behavior	Male occurrences	Female occurrences	p^a
Stand Intermediate	131 (89.7%)	131 (89.7%)	1.00
Walk	81 (55.5%)	99 (67.8%)	0.18
Stand Preen	74 (50.7%)	98 (67.1%)	0.07
Shake Head	72 (49.3%)	60 (41.1%)	0.30
Look at Feet	45 (30.8%)	13 (8.9%)	<0.0001
Shake Wings	4 (2.7%)	47 (32.2%)	<0.0001
Stand Upright	38 (26.0%)	36 (24.7%)	0.82
Head Toss	24 (16.4%)[b]	36 (24.7%)[c]	0.15
Mount/Mounted	10 (6.9%)	10 (6.9%)	0.82
Choke	10 (6.9%)	8 (5.5%)	0.64

[a] Based on chi-square tests comparing the number of male and female occurrences; *df =1*.
[b] 15/24 = 62.5% of Head Toss incidences with no subsequent Mounts.
[c] 26/36 = 72.2% of Head Toss incidences with no subsequent Mounts.

Table 6. Mean duration percentages for common pre- and post-Mount behaviors

	Pre-first-Mount				Post-first-Mount			
	Behavior	Mean % duration	*SD* (%)	*n*	Behavior	Mean % duration	*SD* (%)	*n*
Male	Head Toss	43.4	32.0	133	Stand Interm.	52.8	27.2	131
	Resp. to Beg	51.1	27.0	120	Stand Preen	34.0	26.8	41
	Stand Interm.	11.7	10.6	65	Head Toss	22.4	23.6	23
	Mew	8.4	6.8	47	Look at Feet	18.2	14.7	44
	Walk	7.8	6.0	60	Stand Upright	17.9	16.3	36
	Choke	5.5	4.7	26	Walk	14.0	10.8	81
	Long Call	5.6	3.1	14	Shake Head	6.4	6.0	72
Female	Head Toss	42.4	28.6	136	Stand Interm.	43.5	27.2	129
	Beg	51.5	26.7	120	Stand Preen	41.5	24.4	68
	Choke	11.5	11.0	28	Head Toss	20.9	21.2	34
	Stand Interm.	11.2	9.2	62	Walk	19.1	18.5	95
	Walk	10.9	10.8	49	Stand Upright	18.6	21.7	35
	Mew	7.9	6.0	28	Shake Wings	7.9	6.5	47
	Long Call	6.0	3.2	12	Shake Head	5.1	4.2	60

Table 7. Logistic regression of Mount on environmental factors

Factor	Coefficient (β)	SE[a]	c	OR	95% confidence interval	*p*
Day of the year	0.044	0.006	5	1.245	(1.175, 1.320)	<0.0001
Temperature (ºC)	– 0.024	0.021	5	0.885	(0.724, 1.082)	0.23
Wind speed (m/s)	– 0.041	0.030	1	0.960	(0.905, 1.018)	0.17
Solar elevation (º)	– 0.003	0.002	20	0.936	(0.863, 1.014)	0.11
Tide height (m)	0.195	0.044	1	1.215	(1.115, 1.324)	<0.0001
Eagle disturbance	0.155	0.078	1	1.167	(1.002, 1.360)	0.048
Intercept	– 3.174	0.275				

[a] Adjusted for overdispersion by the variance inflation factor = 1.77.

Table 8. Logistic regression of Paired Head Toss on environmental factors

Factor	Coefficient (β)	SE[a]	c	OR	95% confidence interval	*p*
Day of the year	– 0.007	0.004	5	0.967	(0.934, 1.002)	0.06
Wind speed (m/s)	– 0.049	0.037	1	0.952	(0.886, 1.024)	0.19
Solar elevation (º)	– 0.005	0.002	20	0.899	(0.822, 0.983)	0.02
Tide height (m)	0.125	0.054	1	1.134	(1.019, 1.261)	0.02
Eagle disturbance	0.098	0.100	1	1.103	(0.906, 1.343)	0.33
Intercept	– 2.798	0.556				

[a] Adjusted for overdispersion by the variance inflation factor = 1.23.

Table 9. Logistic regression of Courtship Beg/Respond to Beg on environmental factors

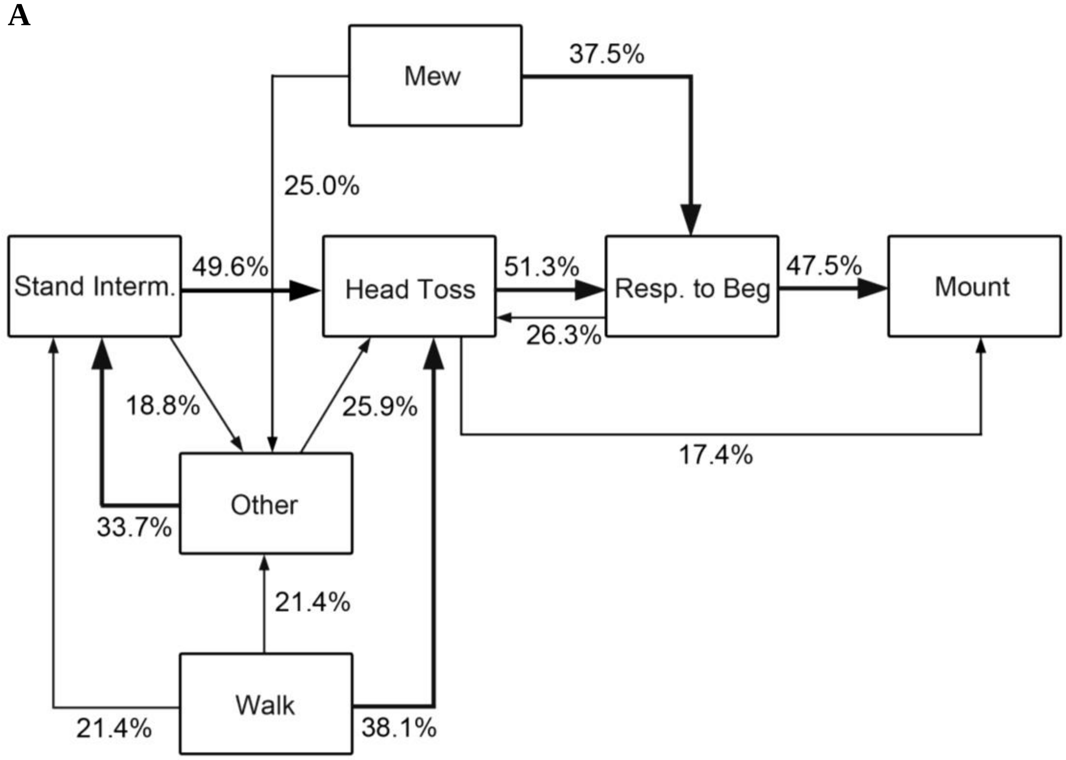
Factor	Coefficient (β)	SE[a]	c	OR	95% confidence interval	*p*
Day of the year	0.077	0.008	5	1.472	(1.364, 1.590)	< 0.0001
Temperature (ºC)	– 0.054	0.028	5	0.765	(0.584, 1.003)	0.053
Solar elevation (º)	0.006	0.002	20	1.136	(1.031, 1.252)	0.01
Tide height (m)	0.138	0.050	1	1.148	(1.040, 1.267)	0.007
Eagle disturbance	0.252	0.088	1	1.287	(1.082, 1.530)	0.005
Intercept	– 4.873	0.371				

[a] Adjusted for overdispersion by the variance inflation factor = 1.29.

Figure 1. Male and female pre-Mount courtship behavior sequences

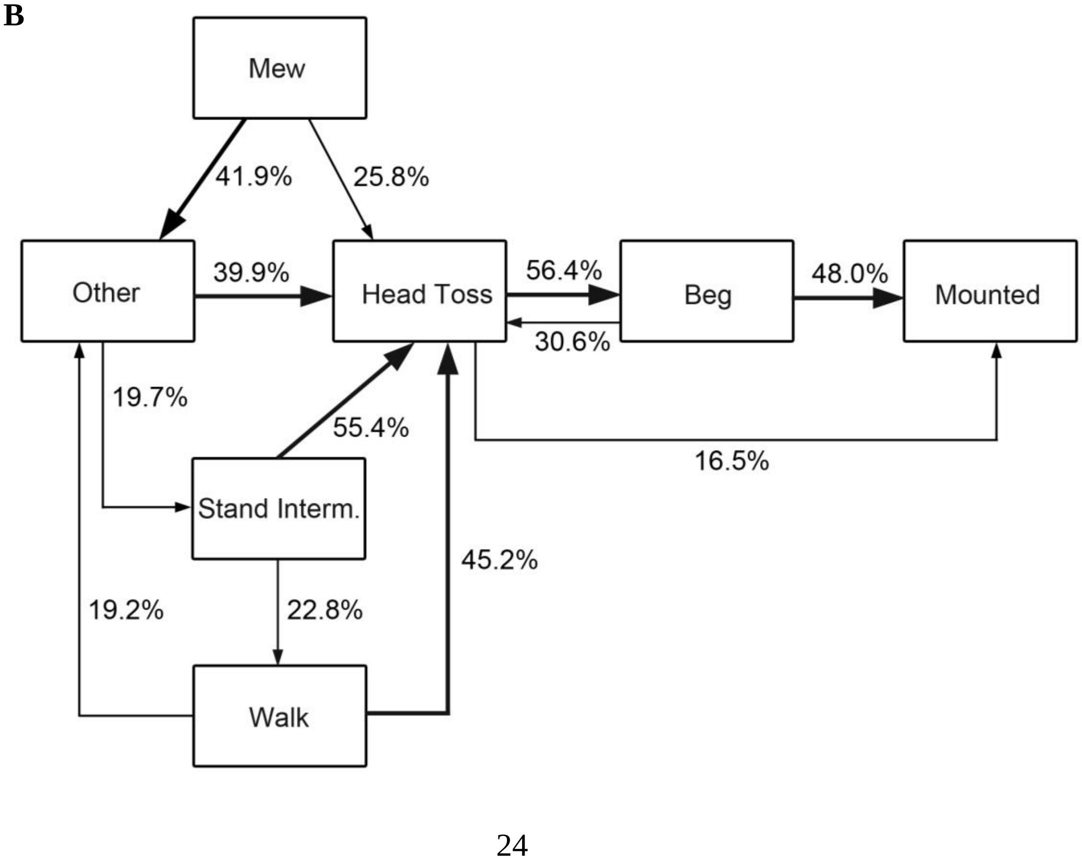
The two behaviors occurring with the highest frequencies following the five most common pre-Mount behaviors are displayed for **A** males and **B** females. Percentages are the occurrences of those two behaviors compared to the total number of all subsequent occurrences. The most frequent behavior following each of the five most common behaviors is preceded by a thicker arrow and the second-most frequent behavior by a thinner arrow.

A



Mew
37.5%
25.0%
Stand Interm.
49.6%
Head Toss
51.3%
Resp. to Beg
47.5%
Mount
26.3%
18.8%
25.9%
17.4%
Other
33.7%
21.4%
Walk
21.4%
38.1%

B



Mew
41.9%
25.8%
Other
39.9%
Head Toss
56.4%
Beg
48.0%
Mounted
30.6%
19.7%
55.4%
16.5%
Stand Interm.
45.2%
19.2%
22.8%
Walk

Figure 2. Integrated male and female pre-Mount courtship behavior sequence

The two behaviors occurring with the highest frequencies immediately follow the opposite gender's most common pre-Mount behaviors. Stand Intermediate and Walk are excluded for clarity. Behaviors preceded by *M* are those of the male; those preceded by *F* are female behaviors. The most frequent behavior following each of the five most common behaviors is preceded by a thicker arrow and the second-most frequent behavior by a thinner arrow. Gray bars indicate the most frequent simultaneously occurring behaviors. Percentages are the occurrences of each subsequent or simultaneous behavior of all subsequent or simultaneous occurrences. The one exception to the above conventions is female Head Toss followed by female Beg as a substitute for male Respond to Beg. Pairs could begin courtship at any point along the sequence prior to Mount.

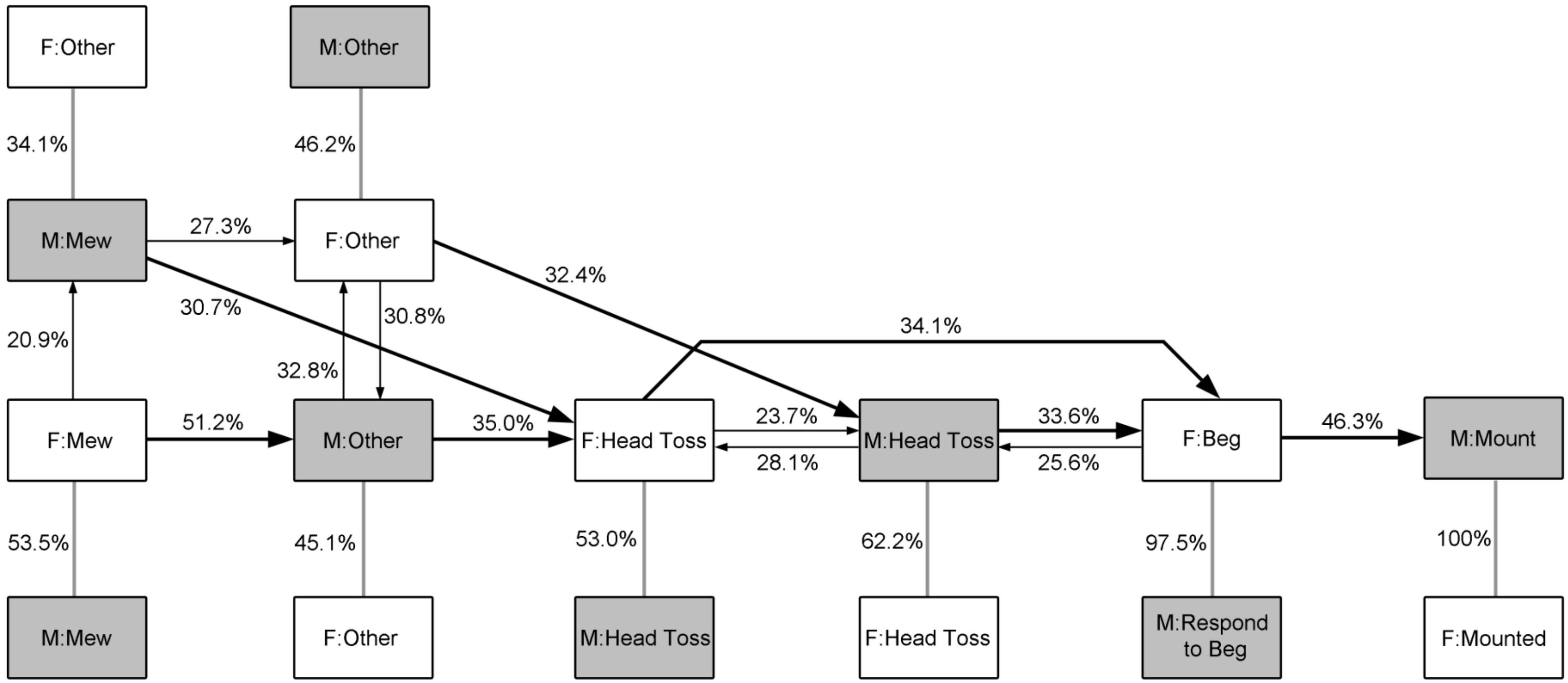
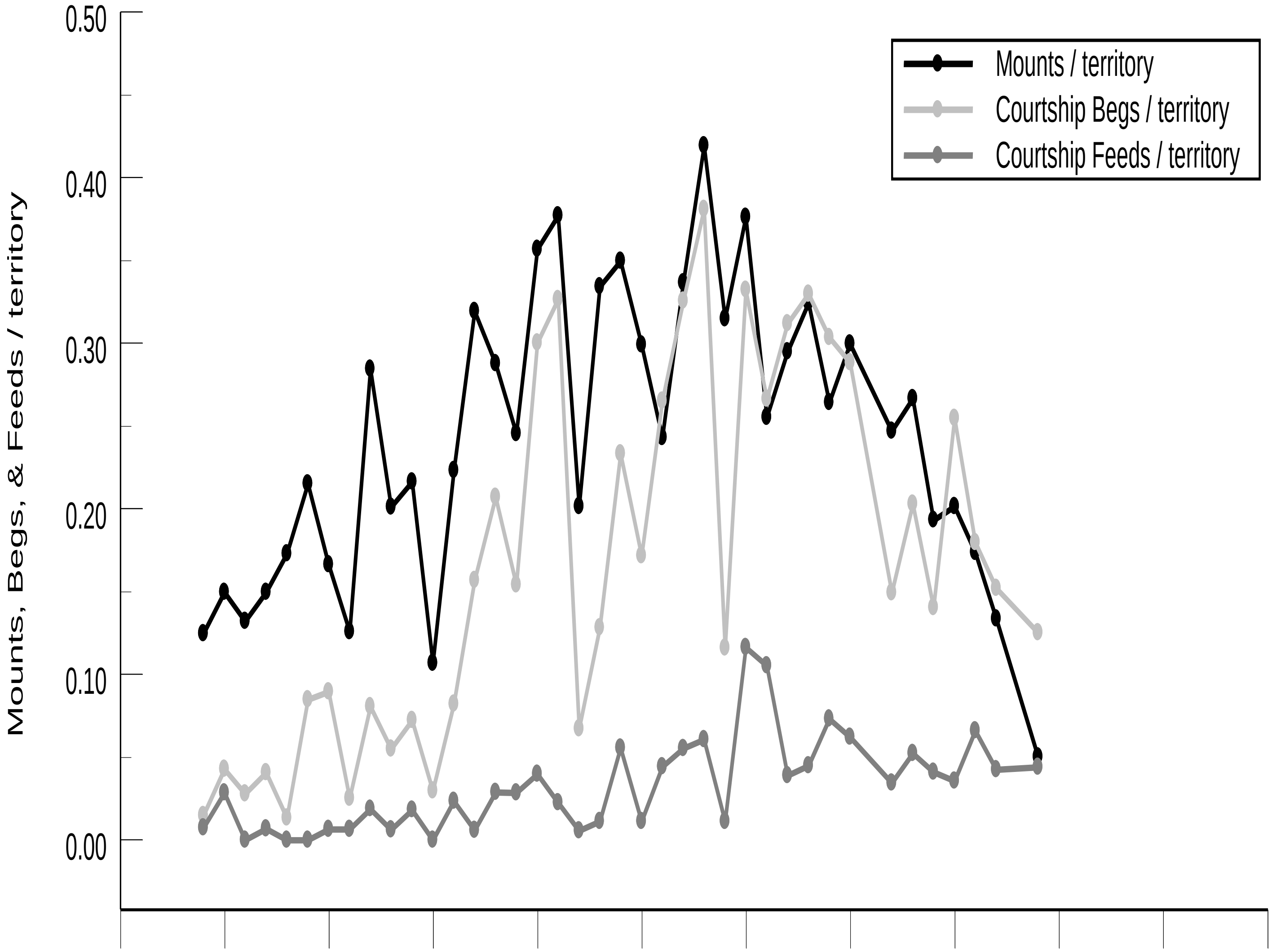

F:Other
M:Other
34.1%
46.2%
M:Mew
27.3%
F:Other
32.4%
30.7%
30.8%
34.1%
20.9%
32.8%
F:Mew
51.2%
M:Other
35.0%
F:Head Toss
23.7%
28.1%
M:Head Toss
33.6%
25.6%
F:Beg
46.3%
M:Mount
53.5%
45.1%
53.0%
62.2%
97.5%
100%
M:Mew
F:Other
M:Head Toss
F:Head Toss
M:Respond
to Beg
F:Mounted

Figure 3. Daily Mounts, Courtship Begs, Courtship Feeds, and clutch initiations per territory during the mating season

Daily per territory Mount, Courtship Beg, Courtship Feed, and clutch initiation incidences observed during 10-min behavior scans for each day of data collection (13 May to 22 June 2008; day 134 to 174 for courtship/Mount scan counts; 13 May to 28 June; day 134 to day 180 for clutch initiation). The peak Courtship Beg and Mount incidence was day 158, 6 June 2008, the peak day of Courtship Feed was day 160, 8 June 2008, and the peak clutch initiation day was 16 June, day 168.


Mounts, Begs, & Feeds / territory
0.50
0.40
0.30
0.20
0.10
0.00
Mounts / territory
Courtship Begs / territory
Courtship Feeds / territory

CHAPTER 4

DISCUSSION

Courtship Behavior Occurrences and Percent Durations

Based on the video data, neither member of the pair is more likely to begin courtship than the other (Table 1). Moreover, the frequencies of various behaviors used by males and females during courtship bouts were similar. The frequencies of the common courtship behaviors, except male Choke, were relatively constant among the three stages of the breeding season, meaning that the relative occurrence of courtship behaviors was conserved over the mating season (Table 10, Appendix). Choke, used also during aggressive encounters (Hayward & Verbeek, 2008), exhibited its lowest frequency during the incubation stage after territory boundaries had become well established. By contrast, Butler and Janes-Butler (1983) found that male great black-backed gulls (*L. marinus*) emitted more Long Calls, Mews, and Chokes after clutch initiation. I cannot substantiate this trend in my study because sampling encompassed only a few days during egg laying and incubation and the sample sizes of these behaviors were relatively low.

The durations of male and female courtship behaviors in relation to the total courtship bout durations remained constant throughout the breeding season (Table 6). These findings could support a reciprocal nature of courtship displays between males and females; at minimum, they imply that males and females spent relatively the same proportion of courtship bouts engaging in the same behaviors. Also, percent durations among the three reproductive stages were not significantly different (Table 17), implying that the total durations of courtship behaviors in relation to the total courtship bout duration remained fairly constant throughout the breeding season.

Courtship Behavior Sequences

Since larids engage in multiple behaviors during courtship, the sequences and the frequencies of these behaviors might be important. For both males and females, Head Toss was the most common initiating courtship behavior (Table 1). When considering the courtship behavior sequences of males and females separately, the most probable male sequence paralleled that of the female after Head Toss (Figure 1). These parallel sequences imply that males and females could be reciprocating each other's courtship behaviors, although, as the differing sets of frequencies for males and females in Figure 1 imply, this reciprocity is not exact. Figure 2 also implies reciprocity between males and females. However, that behaviors of one member of the pair follow the same behaviors of the other does not mean the other bird in the pair is necessarily eliciting the mate's subsequent behaviors. One exception to the proposed reciprocal nature of courtship was that the most common male behavior following female Head Toss was not male Head Toss, but male Respond to Beg, leading to the implied female transition of Head Toss → Courtship Beg. This 'exception' may be due to the artificial designation of Courtship Beg as a separate behavior from Head Toss. Female Courtship Beg and male Respond to Beg are considered to be specialized forms of Head Toss (Hayward & Verbeek, 2008), and either Courtship Beg or Head Toss occurred in every pre-Mount behavior sequence observed. Figure 2 implies that the female initiated the transition of Head Toss to Courtship Beg/Respond to Beg prior to Mount attempts by the male.

Vermeer (1963) found the following reciprocated courtship sequence in herring gulls (*L. argentatus*): Long Call → Grass Pull or Choke → Mew → Head Toss → Copulation or Courtship Feed. By contrast, I did not frequently observe Long Call, Grass Pull, or Choke at the beginning of courtship bouts in glaucous-winged gull pairs; Head Toss, however, almost always preceded Mount. Head Toss was absent from only 6 of the 147 observed courtship bouts. Females singly initiated Head Toss significantly more than males, and together with the female-initiated Head Toss → Beg transition, this implies that females typically initiate behavior transitions within at least the courtship sequence following Head Toss. Tinbergen (1960) observed that herring gull females took the initiative in pair formation courtship displays. He also observed that females initiated Head Toss and suggested that this behavior could help the male identify the female. Other males reacted by running away or threatening, but the female in a pair adopted a submissive posture when she engaged in Head Toss and Beg. In the 6 bouts in which Head Toss did not occur, Courtship Beg initiated the bout, another female-initiated behavior.

Tinbergen (1960) believed that the female, through Head Toss (and Courtship Beg in this study), stimulated the male to Mount. He suggested that a female influenced a male to copulate once he mounted through the summated stimulus of repeated Head Toss against his breast feathers. He also described how a female could motivate a ‘reluctant’ male to initiate cloacal contact by raising her tail feathers after the male had mounted. In the black-headed gull (*Chroicocephalus ridibundus*), Moynihan (1955) observed that the

Head Toss and Beg behaviors preceding successful and unsuccessful Mounts were similar, and suggested that whatever differences between those that determined success or failure came into effect only after Mount. Therefore, behaviors taking place after Mount, such as female Head Toss and tail feather-raising or male contact on the female's back, could be considered courtship behaviors in that they could stimulate successful copulation. In my study, courtship behavior sequences were assumed to end at Mount because the Copulation Call begins just prior to Mount. However, the dividing line between pre-Mount courtship, Mount, and copulation is not clear. Males do rape females, however, perhaps sometimes inadvertently in response to female Courtship Beg. Most instances of rape are male-initiated, however, so female stimulation is not necessary to motivate males to attempt copulation (Hayward & Verbeek, 2008). In the present study, males and females simultaneously (at the resolution of observation) began to Head Toss during 30 courtship bouts, demonstrating the tight communication between members of pairs. A higher-resolution method of observation would be needed to determine which member of the pair initiated these courtship sequences.

Mount and Copulation

Numbers of first Mounts during the morning versus evening recordings during the three stages were significantly different from expected (Table 3), with the pre-egg-laying and incubation stages having more first Mounts in the mornings but the egg-laying stage having approximately equal numbers of Mounts in the morning and evening. The egg-laying stage also contained the highest (although not significantly) average copulation duration, wing-flag duration, and number of cloacal contacts, as well as the highest number of sequential Mounts. The total number of first Mounts by stage were significantly different from expected because there were more Mounts than expected during the egg-laying stage and fewer Mounts than expected during incubation stage. All these results imply that the drive to copulate, presumably a reflection of hormone levels, is highest during the egg-laying stage, resulting in more Mounts overall and comparatively more Mounts during the evening than earlier or later in the mating season. Figure 3 shows that the peak number of Mounts/territory occurred 10 days before the peak clutch initiations on 4 June 2008 (day 156). Brown (1967) estimated that ovarian follicles in lesser black-backed gulls (*L. fuscus*) started accelerated growth 10 days before laying. He suggested that one of the functions for the multiple copulations before laying is to stimulate the final growth of the follicles, since at that point there is nothing to fertilize.

During the three stages of the mating season, the gulls exhibited consistent copulation duration, wing flag duration, number of cloacal contacts per copulation, and copulation success (Table 3). Brown (1967) found that lesser black-backed gulls also experienced relatively consistent Mount success and number of cloacal contacts per copulation, though he only observed the pre-egg-laying stage. The percentage of Mounts that ended in successful copulations did not significantly deviate from the expected but was highest in the pre-egg-laying stage, again perhaps a reflection of hormone levels. Burger (1976) found that mean copulation duration and frequency increased during the pre-egg-laying period for laughing gulls (*Leucophaeus atricilla*); my data collection did not encompass multiple days during the pre-laying period, so I cannot substantiate this for glaucous-winged gulls. But copulation duration was slightly longer, though non-significantly so, during the egg-laying stage. Why significantly more Mounts occurred in the morning versus the evening is less obvious, perhaps relating to some endogenous or exogenous cycle. Data collected over the entire mating season might allow for more conclusive results.

In no day sampled were Mounts in 5-min intervals significantly clustered. Using similar methods to mine, Brown (1967) found localized mounting synchronization in lesser black-backed gulls, and Gochfeld (1980) found temporal clustering of precopulatory and copulatory displays in common terns (*Sterna hirundo*). I would need to sample a larger area and multiple days around the peak Mount day to detect Mount clustering and/or synchrony.

Post-Mount Behaviors

Following the first Mount, pairs typically resumed feather maintenance or resting, or they exited the territory. If the first Mount was not successful, males sometimes engaged in further Mount attempts. Once a successful copulation was achieved, however, I observed no further Mount attempts. The most multiple Mounts were observed during the middle of the breeding season (Table 3), probably due to hormone levels and perhaps to the synergistic effects of socially facilitated displays suggested by Brown 1967. Male and female behaviors after the first Mount also displayed equivalent occurrences, except that males exhibited a higher occurrence of Look at Feet and females exhibited a higher occurrence of Shake Wings (Table 5). Shake Wings represents an attempt by the female to rearrange her feathers after a Mount. Tinbergen (1960) observed Look at Feet, but its function has not been investigated. During this behavior, an individual looks down at its feet with its bill pointing toward the ground for up to an observed maximum of 26 sec. Tinbergen (1960) suggested that this behavior could be involved with keeping the feet clean. Females during the incubation stage had a higher (though not significant) incidence of Look at Feet (Table 15 and Table 16, Appendix), so it could possibly be related to nest material gathering or egg laying.

Behaviors following the first Mount exhibited relatively consistent percent durations in relation to total after-Mount durations. Also, for both males and females, Head Toss and Choke occurred both before and after the first Mount, often without any subsequent Mount attempts (Table 5). For both males and females, mean Head Toss percent duration in relation to the total post-first-Mount duration was significantly less than pre-Mount Head Toss percent duration (Table 6), and Courtship Beg never followed post-Mount Head Toss. This result implies a difference in function for this display before and after a Mount. Moynihan (1962) in gray gulls (*Leucophaeus modestus*) and Weidmann (1955) in common gulls (*L. canus*) reported observing post-Mount Head Toss as well. Perhaps post-Mount Head Toss is due to the recent stimulation of a Mount or is a component of general pair bonding such as during pair formation and the greeting ceremony.

Environmental Effects on Courtship and Mount

I was interested in the effects of both social and environmental factors on courtship and Mount. My results suggest that Mount depends on environmental factors influencing social interaction and sex hormone levels. The effect of day of year, a factor that was predicated on the peak Mount day, was likely related to the effect of photoperiod on hormone levels. In temperate climates, long days are important in synchronizing breeding activity with the season when food is most abundant and conditions are favorable for raising young (Ball & Balthazart, 2004). At least during the chick-rearing season, tide and colony attendance are directly related (Henson et al., 2007). Intra- and inter-pair social interaction presumably increases with territory attendance, which is closely related to colony attendance; therefore, tide could be affecting social interaction. In many birds, visual and social stimuli influence sexual responses by modulating hormone levels (Ball & Balthazart, 2004). Photoperiod supplies initial cues to initiate gonad growth, but cues such as mild weather, nest site availability, food availability, and social cues fine-tune this response to allow egg laying to be optimally timed to local conditions (Ball & Ketterson, 2007). Burger (1976) indicated that copulation frequency was higher in the morning and evening in laughing gulls, but in glaucous-winged gulls, tide height seemed to override the effect of solar elevation. Brown (1967) found that daily Mount frequency in lesser black-backed gulls was significantly correlated with date but not with mean temperature (10 days earlier when follicle growth started) or hours of sunlight, a finding similar to my results.

Interestingly, eagle disturbance had a positive effect on the incidence of Mount, perhaps because it promoted greeting ceremonies as pairs returned to their territories after the disturbance, which segued into courtship and Mount. Brown (1967) found that copulation 'luring' behaviors (Mew, Choke, and Head Toss) were linked with the greeting ceremony. Another possibility is that the comfort behaviors in which individuals engage after arriving back on territory after a disturbance, such as wing flapping and tail-wagging, could be similar enough to movements during copulation to stimulate courtship and Mount. More in-depth data collection will be needed to clarify why an increase in Mount occurs in response to eagle disturbance.

Only solar elevation and tide height affected Paired Head Toss; higher solar elevations depressed the odds of Head Toss, and increased tide height increased the odds. Therefore, Paired Head Toss, as interpreted in this study, appears to be primarily influenced by factors related to colony attendance. Unlike for Mount, Head Toss was not affected by day of year and eagle disturbance, perhaps because Head Toss is not exclusively a precopulatory behavior. Head Toss is also used during the greeting ceremony and as a pair-bonding behavior (Hayward & Verbeek, 2008).

Courtship Beg was affected in the same manner by the same factors as Mount, with the addition of solar elevation. These similarities are not surprising since Courtship Beg/Respond to Beg is often the preliminary behavior before Mount and implies that, as for Mount, the environment is also influencing hormonal levels and social interactions. However, unlike Paired Head Toss, Courtship Beg increased in response to increased solar elevation, instead of decreasing. Why this relation existed is uncertain. Courtship Beg also peaked on the same day as Mount (day 158; 6 June 2008; Figure 3). Figure 3 shows that this peak day occurred 10 days before the peak day of clutch initiation (day 168; 16 June 2008). Brown (1967) found similar results for lesser black-backed gulls. What I considered Courtship Beg was clearly a type of Head Tossing linked to Mounts. Courtship Beg, however, is not an exclusive precopulatory behavior, as the female uses it to beg for food at other times.

These conclusions can be applied only to the 2008 breeding season. Events that might change the factors used in the regression models, such as El Niño and La Niña Southern Oscillation events or increasing eagle disturbance, would affect logistic model parameters and potentially the behaviors of the gulls.

Courtship Feed

Peak Courtship Feed occurred 2 days after peak Courtship Beg and Mount (Figure 3). Courtship Feed has both a display function in courtship and physical function in providing the female food, and in black-headed gulls, the female was the main initiator in eliciting a Feed from a male (Moynihan, 1955). Its social role could extend from inducing successful copulations to extending the pair bond to the next year's breeding season (Tasker & Mills, 1981). Salzer & Larkin (1990) reported that in glaucous-winged gulls, Courtship Feed increased steadily during the pre-laying period, peaked 2 days before egg laying, and then decreased abruptly after the first egg was laid. Figure 3 shows that the peak Courtship Feed day preceded the peak clutch initiation day by 8 days, perhaps because my method of data collection used scan counts and not observation of individual pairs. The peak Courtship Feed day followed the peak Mount and Courtship Beg day by 2 days. Courtship Beg, a signal for Courtship Feed and Mount, appears to be the same display (Tinbergen, 1960), perhaps to keep the follicle-stimulating (Mount) and food-providing (Courtship Feed) systems in phase (Brown, 1967). For glaucous-winged gulls, Vermeer (1963) suggested an appeasement function for Courtship Feed. Brown (1967) found that lesser black-backed gulls could be induced to continue to copulate and Courtship Feed if eggs were removed, so clutch presence could be important in regulating courtship and copulation. Obviously Courtship Feed has some functional relation to Copulation and egg laying, and, at minimum, my results show that it provided females with additional food during most of the egg-formation period.

Courtship and Fitness

Both pre-Mount and post-Mount male and female behavior occurrences and percent durations showed no significant differences, implying some sort of mutual display between the two individuals in a pair. Pre-Mount courtship behaviors appear to be reciprocated between the female and male, a sort of call-and-response conversation with transitions initiated by the female after Head Toss. Since the female appears to be the catalyst of courtship progression, it is imperative that she receives the proper stimuli at the proper time to initiate sex hormone production, to drive her to engage in courtship, and eventually to accelerate follicle growth. These stimuli could include a complex interplay of female and male communication and environmental cues such as day length, tide height, and time of day. Some evidence suggests that multiple copulations play a role in accelerating follicle growth and that Courtship Feed influences Mount success and pair bonding, so inter-pair communication could have far-reaching consequences (Brown, 1967; Tasker & Mills, 1981). Therefore, a pair's courtship communication could influence the quality and longevity of the pair bond, the probability of Mounts, and the prospect of successful copulations, all of which could impact reproductive fitness. The call-and-response sequence of courtship displays between a pair could contagiously transfer to neighboring pairs, since these gulls live in large colonies with closely spaced territories where social interaction is a given. Evidence suggests that this inter-pair communication influences hormone levels, resulting in local synchrony of courtship and copulation, which could translate to the colony as a whole (Brown, 1967; Southern, 1974; Gochfeld, 1980; Ball & Balthazart, 2004; Ball & Ketterson, 2007). Environmental cues could therefore affect inter-pair communication and result in colony-wide synchrony of reproductive activities. Apart from other advantages, this colonial synchrony can impact the fitness of nesting birds (Clayton, 1978).

Seasonal Reproductive Synchrony

Courtship and Mount/copulation activities were synchronized during the breeding season, resulting in peak levels of daily Mount, Courtship Beg, Courtship Feed, and clutch initiation (Figure 3). To optimize breeding success in a temperate climate, individuals in the colony must reproduce at the optimal time of year. Individuals also must respond to increasing levels of bald eagle predation (Hayward et al., 2010). The increased odds of Mount and Courtship Beg with eagle disturbance is especially interesting in this context. Eagle disturbance apparently influences the frequency of gull courtship and mating behavior and perhaps their overall activity and energy budgets. The mechanism behind the increase in the odds for these behaviors would be interesting to explore. For example, is this increase merely due to the disturbance-induced concurrent return of a large number of pairs that subsequently and independently engage in greeting ceremonies, or is it due to a more complex scenario involving mass social facilitation? Also, does this effect continue into the incubation season and possibly change the dynamics of hormone levels and influence egg laying or incubation?

Seasonal mating behavior synchrony could be socially produced from behavior interactions, be some adaptation to environmental conditions, or especially in temperate climates, be some combination of the two. At least for the days sampled with video analysis, localized social facilitation of Mount does not seem to be occurring, but this may be a limitation of the sampling time and area. The relative contributions of social facilitation and hormone levels to the promotion of courtship displays, copulation, and egg laying need further study. On the basis of this study, the environmental factors of day of year (a proxy of photoperiod), tide height, and solar elevation are the primary contributors to daily and seasonal incidences of courtship and copulation in glaucous-winged gulls, although, surprisingly, eagle disturbance plays a role. However, males and females may not respond in the same manner to these environmental cues. Evidence suggests that females play a greater role in 'fine-tuning' reproductive responses to the environment. Ultimately, the female, not the male, makes the critical response of egg laying to local and yearly resource variability. In many males, photoperiod alone is enough to induce reproductive readiness. However, females require a combination of photoperiod to initiate ovarian development and supplementary cues to commence exponential growth and yolk deposition. The female's behavior can influence the timing of male breeding, but the reverse does not seem to be true (Ball & Ketterson, 2008). This seasonal timing dictated by the female could even extend down to the female's role in initiating transitions within the pre-Mount courtship sequence.

Understanding the dynamics of courtship and copulation behaviors and sequences in relation to social and environmental cues can give insights into the specific factors influencing overall breeding success. Also, colonial waterbirds such as the glaucous-winged gull can be used as biological indicators of environmental change (Kushlan, 1993), so a greater understanding of their breeding biology could prove to be valuable.

APPENDIX

EXPANDED DATA FOR THREE STAGES OF THE MATING SEASON

Table 10. Occurrences of common pre-Mount courtship behaviors during three stages of the breeding season

	Male					Female				
Behavior	Pre-egg-laying stage	Egg-laying stage	Incubation stage	χ^2	*p*	Pre-egg-laying stage	Egg-laying stage	Incubation stage	χ^2	*p*
First Mount	49 (100.0%)	58 (100.0%)	40 (100.0%)			49 (100.0%)	58 (100.0%)	40 (100.0%)		
Head Toss	44 (89.8%)	55 (94.8%)	36 (90.0%)	0.09	0.95	46 (93.9%)	55 (94.8%)	37 (92.5%)	0.01	0.99
Beg/Resp. to Beg	37 (75.5%)	49 (84.5%)	35 (87.5%)	0.44	0.80	38 (77.6%)	49 (84.5%)	34 (85.0%)	0.20	0.90
Stand Interm.	28 (57.1%)	28 (48.3%)	14 (35.0%)	2.28	0.32	18 (36.7%)	32 (55.1%)	13 (32.5%)	3.48	0.18
Walk	15 (30.6%)	29 (50.0%)	18 (45.0%)	2.47	0.29	16 (32.7%)	23 (39.7%)	10 (25.0%)	1.54	0.46
Mew	19 (38.8%)	17 (29.3%)	15 (37.5%)	0.54	0.76	14 (28.6%)	11 (19.0%)	5 (12.5%)	2.88	0.24
Choke	9 (18.4%)	9 (15.5%)	0 (0.0%)	6.91	0.03	9 (18.4%)	6 (10.3%)	1 (2.5%)	5.12	0.08
Long Call	6 (12.2%)	8 (13.8%)	1 (2.5%)	3.26	0.20	5 (10.2%)	6 (10.3%)	1 (2.5%)	2.16	0.34
Courtship Feed	4 (8.2%)	6 (10.3%)	3 (7.5%)	0.26	0.88	4 (8.2%)	6 (10.3%)	2 (5.0%)	0.83	0.66

[a] χ^2 expected values generated by determining the proportion of each stage's courtship bouts of the total, then multiplying that value by the total number of occurrences of each behavior; $df = 2$.

Table 11. Occurrences of common male pre-Mount behaviors immediately before and after each other by stage of the mating season

Male behavior:	before 80 82	before 80 12	before 80 42	before 80 70	before 80 71	before sum	before 80 other	after 80 82	after 80 12	after 80 42	after 80 70	after 80 71	after 80 84	after 80 sum	after 80 other
Total	52	66	32	5	2	157	50	136	23	16	3	6	46	230	35
Pre-egg-laying	13	27	2	2	1	45	16	33	13	2	2	3	17	70	11
Egg-laying	22	26	16	1	1	66	23	56	6	12	1	2	20	97	14
Incubation	17	13	14	2	0	46	11	47	4	2	0	1	9	63	10
Total %	25.1%	31.9%	15.5%	2.42%	1.0%	75.8%	24.1%	51.3%	8.68%	6.0%	1.1%	2.3%	17.4%	86.8%	13.2%
				70+71:	3.4%										

Male behavior:	before 82 80	before 82 12	before 82 42	before 82 70	before 82 71	before sum	before 82 other	after 82 80	after 82 12	after 82 42	after 82 70	after 82 71	after 82 84	after 82 sum	after 82 other
Total	136	11	10	5	13	175	18	52	8	13	1	1	94	169	29
Pre-egg-laying	33	5	4	0	9	51	7	13	6	3	0	1	29	52	7
Egg-laying	56	5	3	3	1	68	7	22	0	6	0	0	35	63	14
Incubation	47	1	3	2	3	56	4	17	2	4	1	0	30	54	8
Total %	70.5%	5.7%	5.2%	2.6%	6.7%	90.7%	9.3%	26.3%	4.0%	6.6%	0.5%	0.5%	47.5%	85.4%	14.7%

Male behavior:	before 12 80	before 12 82	before 12 42	before 12 70	before 12 71	before sum	before 12 other	after 12 80	after 12 82	after 12 42	after 12 70	after 12 71	after 12 84	after 12 sum	after 12 other
Total	23	8	18	2	4	55	65	66	11	21	4	3	3	108	25
Pre-egg-laying	13	6	8	0	1	28	29	27	5	11	1	2	2	48	14
Egg-laying	6	0	8	1	2	17	26	26	5	8	1	0	1	41	8
Incubation	4	2	2	1	1	10	10	13	1	2	2	1	0	19	3
Total %	19.2%	6.7%	15.0%	1.7%	3.3%	45.8%	54.2%	49.6%	8.3%	15.8%	3.0%	2.3%	2.3%	81.2%	18.8%

Male behavior:	before 42 80	before 42 82	before 42 12	before 42 70	before 42 71	before sum	before 42 other	after 42 80	after 42 82	after 42 12	after 42 70	after 42 71	after 42 84	after 42 sum	after 42 other
Total	16	13	21	1	4	55	60	32	10	18	1	4	1	66	18
Pre-egg-laying	2	3	11	1	1	18	19	2	4	8	0	2	0	16	7
Egg-laying	12	6	8	0	0	26	31	16	3	8	0	1	1	29	10
Incubation	2	4	2	0	3	11	10	14	3	2	1	1	0	21	1
Total %	13.9%	11.3%	18.3%	0.9%	3.5%	47.8%	52.2%	38.1%	11.9%	21.4%	1.2%	4.8%	1.2%	78.6%	21.4%

Table 11. – *Continued.*

Male behavior:	before 70 80	before 70 82	before 70 12	before 70 42	before 70 71	before sum	before 70 other	after 70 80	after 70 82	after 70 12	after 70 42	after 70 71	after 70 84	after 70 sum	after 70 other
Total	3	1	4	1	0	9	3	5	5	2	1	7	0	20	2
Pre-egg-laying	2	0	1	0	0	3	1	2	0	0	1	3	0	6	1
Egg-laying	1	0	1	0	0	2	2	1	3	1	0	1	0	6	0
Incubation	0	1	2	1	0	4	0	2	2	1	0	3	0	8	1
Total %	25.0%	8.3%	33.3%	8.3%	0.0%	75.0%	25.0%	22.7%	22.7%	9.1%	4.6%	31.8%	0.0%	90.9%	9.1%

Male behavior:	before 70+71 80	before 70+71 82	before 70+71 12	before 70+71 42	before 70+71 70	before sum	bf 70+71 other	after 70+71 80	after 70+71 82	after 70+71 12	after 70+71 42	after 70+71 70	after 70+71 84	aft 70+71 sum	aft 70+71 other
Total %	26.4%	5.9%	20.6%	14.7%			32.4%	14.6%	37.5%	12.5%	10.4%		0.0%		25.0%

Male behavior:	before 71 80	before 71 82	before 71 12	before 71 42	before 71 70	before sum	before 71 other	after 71 80	after 71 82	after 71 12	after 71 42	after 71 70	after 71 84	after 71 sum	after 71 other
Total	6	1	3	4	7	21	8	2	13	4	4	7	0	30	10
Pre-egg-laying	3	1	2	2	3	11	4	1	9	1	1	3	0	15	5
Egg-laying	2	0	0	1	1	4	2	1	1	2	0	1	0	5	4
Incubation	1	0	1	1	3	6	2	0	3	1	3	3	0	10	1
Total %	20.7%	3.45%	10.3%	13.8%	24.1%	72.4%	27.6%	5.0%	32.5%	10.0%	10.0%	17.5%	0.0%	75.0%	25.0%

Male behavior:	before other 80	before other 82	before other 12	before other 42	before other 70+71	before sum	before other other	after other 80	after other 82	after other 12	after other 42	after other 70+71	after other 84	after other sum	after other other
Total	35	29	25	18	12	119	37	50	18	65	10	11	2	156	37
Pre-egg-laying	11	7	14	7	6	45	16	16	7	29	3	5	1	61	16
Egg-laying	14	14	8	10	4	50	18	23	7	26	5	4	0	65	18
Incubation	10	8	3	1	2	24	3	11	4	10	2	2	1	30	3
Total %	22.4%	18.6%	16.0%	11.5%	7.7%	76.3%	23.7%	25.9%	9.3%	33.7%	5.2%	5.7%	1.0%	80.8%	19.2%

Legend: 80 = Head Toss; 82 = Respond to Beg; 12 = Stand Intermediate; 42 = Walk; 70 = Mew; 71 = Mew Toward; Other = any other behavior besides the previous.

Table 12. Occurrences of common female pre-Mount behaviors immediately before and after each other by stage of the mating season

Female behavior:	before 80 81	before 80 12	before 80 42	before 80 70	before 80 71	before sum	before 80 other	after 80 81	after 80 12	after 80 42	after 80 70	after 80 71	after 80 85	after 80 sum	after 80 other
Total	60	56	33	3	5	157	69	164	22	21	1	4	48	260	31
Pre-egg-laying	19	17	11	1	3	51	23	49	4	7	1	2	18	81	16
Egg-laying	24	22	16	1	2	65	31	66	12	9	0	2	20	109	9
Incubation	17	17	6	1	0	41	15	49	6	5	0	0	10	70	6
Total %	26.6%	24.8%	14.6%	1.3%	2.2%	69.5%	30.5%	56.4%	7.6%	7.2%	0.3%	1.4%	16.5%	89.3%	10.7%

Female behavior:	before 81 80	before 81 12	before 81 42	before 81 70	before 81 71	before sum	before 81 other	after 81 80	after 81 12	after 81 42	after 81 70	after 81 71	after 81 85	after 81 sum	after 81 other
Total	164	3	10	0	3	180	10	60	16	7	0	0	94	177	19
Pre-egg-laying	49	0	4	0	2	55	5	19	4	4	0	0	30	57	4
Egg-laying	66	0	4	0	1	71	2	24	3	3	0	0	35	65	10
Incubation	49	3	2	0	0	54	3	17	9	0	0	0	29	55	5
Total %	86.3%	1.6%	5.3%	0.0%	1.6%	94.7%	5.3%	30.6%	8.2%	3.6%	0.0%	0.0%	48.0%	90.3%	9.7%

Female behavior:	before 12 80	before 12 81	before 12 42	before 12 70	before 12 71	before sum	before 12 other	after 12 80	after 12 81	after 12 42	after 12 70	after 12 71	after 12 85	after 12 sum	after 12 other
Total	22	16	11	3	2	54	34	56	3	23	1	1	1	85	16
Pre-egg-laying	4	4	2	1	0	11	11	17	0	5	1	0	0	23	4
Egg-laying	12	3	4	0	2	21	21	22	0	15	0	0	0	37	11
Incubation	6	9	5	2	0	22	2	17	3	3	0	1	1	25	1
Total %	25.0%	18.2%	12.5%	3.4%	2.3%	61.4%	38.6%	55.5%	3.0%	22.8%	1.0%	1.0%	1.0%	84.2%	15.8%

Female behavior:	before 42 80	before 42 81	before 42 12	before 42 70	before 42 71	before sum	before 42 other	after 42 80	after 42 81	after 42 12	after 42 70	after 42 71	after 42 85	after 42 sum	after 42 other
Total	21	7	23	0	2	53	65	33	10	11	0	5	0	59	14
Pre-egg-laying	7	4	5	0	0	16	21	11	4	2	0	2	0	19	4
Egg-laying	9	3	15	0	0	27	33	16	4	4	0	2	0	26	8
Incubation	5	0	3	0	2	10	11	6	2	5	0	1	0	14	2
Total %	17.8%	5.9%	19.5%	0.0%	1.7%	44.9%	55.1%	45.2%	13.7%	15.1%	0.0%	6.9%	0.0%	80.8%	19.2%

Table 12. – *Continued.*

Female behavior:	before 70 80	before 70 81	before 70 12	before 70 42	before 70 71	before sum	before 70 other	after 70 80	after 70 81	after 70 12	after 70 42	after 70 71	after 70 85	after 70 sum	after 70 other
Total	1	0	1	0	1	3	4	3	0	3	0	2	0	8	0
Pre-egg-laying	1	0	1	0	0	2	2	1	0	1	0	2	0	4	0
Egg-laying	0	0	0	0	1	1	0	1	0	0	0	0	0	1	0
Incubation	0	0	0	0	0	0	2	1	0	2	0	0	0	3	0
Total %	14.3%	0.0%	14.3%	0.0%	14.3%	42.9%	57.1%	37.5%	0.0%	37.5%	0.0%	25.0%	0.0%	100.0%	0.00%

Female behavior:	before 71 80	before 71 81	before 71 12	before 71 42	before 71 70	before sum	before 71 other	after 71 80	after 71 81	after 71 12	after 71 42	after 71 70	after 71 85	after 71 sum	after 71 other
Total	4	0	1	5	2	12	7	5	3	2	2	2	0	14	13
Pre-egg-laying	2	0	0	2	2	6	3	3	2	0	0	2	0	7	6
Egg-laying	2	0	0	2	0	4	2	2	1	2	0	0	0	5	5
Incubation	0	0	1	1	0	2	2	0	0	0	2	0	0	2	2
Total %	21.1%	0.0%	5.3%	26.3%	10.5%	63.2%	36.8%	18.5%	11.1%	7.4%	7.4%	7.4%	0.0%	51.9%	48.2%

Female behavior:	before other 80	before other 81	before other 12	before other 42	before other 70+71	before sum	before other other	after other 80	after other 81	after other 12	after other 42	after other 70+71	after other 85	after other sum	after other other
Total	31	19	16	14	12	92	33	69	10	34	14	11	2	140	33
Pre-egg-laying	16	4	4	4	6	34	13	23	5	11	5	5	1	50	13
Egg-laying	9	10	11	8	4	42	12	31	2	21	6	2	1	63	12
Incubation	6	5	1	2	2	16	8	15	3	2	3	4	0	27	8
Total %	24.8%	15.2%	12.8%	11.2%	9.6%	73.6%	26.4%	39.9%	5.8%	19.7%	8.1%	6.4%	1.2%	80.9%	19.1%

Legend: 80 = Head Toss; 81 = Courtship Beg; 12 = Stand Intermediate; 42 = Walk; 70 = Mew; 71 = Mew Toward; Other = any other behavior besides the previous.

Table 13. Common male courtship behaviors before, during, and after common female pre-Mount behaviors

Female behavior	Male behavior	# before	# during	# after	Before %	During %	After %
Stand Interm.	Stand Interm.	19	41	35	15.97%	31.06%	26.52%
	Walk	1	2	1	0.84%	1.52%	0.76%
	Mew	7	4	5	5.88%	3.03%	3.79%
	Head Toss	25	41	57	21.01%	31.06%	43.18%
	Resp. to Beg	16	0	3	13.45%	0.00%	2.27%
	Mount	0	0	1	0.00%	0.00%	0.76%
	Other	51	44	30	42.86%	33.33%	22.73%
Walk	Stand Interm.	3	3	3	20.00%	10.34%	10.34%
	Walk	0	0	0	0.00%	0.00%	0.00%
	Mew	0	1	1	0.00%	3.45%	3.45%
	Head Toss	5	17	15	33.33%	58.62%	51.72%
	Resp. to Beg	0	0	0	0.00%	0.00%	0.00%
	Mount	0	0	0	0.00%	0.00%	0.00%
	Other	7	8	10	46.67%	27.59%	34.48%
Mew	Stand Interm.	4	2	3	11.11%	4.65%	6.98%
	Walk	0	0	0	0.00%	0.00%	0.00%
	Mew	11	23	9	30.56%	53.49%	20.93%
	Head Toss	5	4	6	13.89%	9.30%	13.95%
	Resp. to Beg	0	0	3	0.00%	0.00%	6.98%
	Mount	0	0	0	0.00%	0.00%	0.00%
	Other	16	14	22	44.44%	32.56%	51.16%
Head Toss	Stand Interm.	84	75	47	20.69%	15.89%	9.96%
	Walk	9	9	6	2.22%	1.91%	1.27%
	Mew	27	29	20	6.65%	6.14%	4.24%
	Head Toss	113	250	112	27.83%	52.97%	23.73%
	Resp. to Beg	59	0	161	14.53%	0.00%	34.11%
	Mount	0	0	50	0.00%	0.00%	10.59%
	Other	114	109	76	28.08%	23.09%	16.10%
Courtship Beg	Stand Interm.	11	0	8	5.58%	0.00%	3.94%
	Walk	0	0	1	0.00%	0.00%	0.49%
	Mew	19	1	2	9.64%	0.49%	0.99%
	Head Toss	135	0	52	68.53%	0.00%	25.62%
	Resp. to Beg	4	198	5	2.03%	97.54%	2.46%
	Mount	0	0	94	0.00%	0.00%	46.31%
	Other	28	4	41	14.21%	1.97%	20.20%
Mounted	Stand Interm.	3	0	N/A	2.05%	0.00%	N/A
	Walk	0	0	N/A	0.00%	0.00%	N/A
	Mew	0	0	N/A	0.00%	0.00%	N/A
	Head Toss	47	0	N/A	32.19%	0.00%	N/A
	Resp. to Beg	93	0	N/A	63.70%	0.00%	N/A
	Mount	0	147	N/A	0.00%	100.00%	N/A
	Other	3	0	N/A	2.05%	0.00%	N/A
Other	Stand Interm.	42	45	55	15.11%	14.15%	17.30%
	Walk	7	6	4	2.52%	1.89%	1.26%
	Mew	24	30	37	8.63%	9.43%	11.64%
	Head Toss	72	90	103	25.90%	28.30%	32.39%
	Resp. to Beg	26	0	20	9.35%	0.00%	6.29%
	Mount	0	0	1	0.00%	0.00%	0.31%
	Other	107	147	98	38.49%	46.23%	30.82%

Table 14. Common female courtship behaviors before, during, and after common male pre-Mount behaviors

Male behavior	Female behavior	# before	# during	# after	Before %	During %	After %
Stand Interm.	Stand Interm.	35	41	19	23.18%	24.70%	11.45%
	Walk	3	3	3	1.99%	1.81%	1.81%
	Mew	3	2	4	1.99%	1.20%	2.41%
	Head Toss	47	75	84	31.13%	45.18%	50.60%
	Beg	8	0	11	5.30%	0.00%	6.63%
	Mounted	0	0	3	0.00%	0.00%	1.81%
	Other	55	45	42	36.42%	27.11%	25.30%
Walk	Stand Interm.	1	2	1	8.33%	11.76%	5.88%
	Walk	0	0	0	0.00%	0.00%	0.00%
	Mew	0	0	0	0.00%	0.00%	0.00%
	Head Toss	6	9	9	50.00%	52.94%	52.94%
	Beg	1	0	0	8.33%	0.00%	0.00%
	Mounted	0	0	0	0.00%	0.00%	0.00%
	Other	4	6	7	33.33%	35.29%	41.18%
Mew	Stand Interm.	5	4	7	6.76%	4.55%	7.95%
	Walk	1	1	0	1.35%	1.14%	0.00%
	Mew	9	23	11	12.16%	26.14%	12.50%
	Head Toss	20	29	27	27.03%	32.95%	30.68%
	Beg	2	1	19	2.70%	1.14%	21.59%
	Mounted	0	0	0	0.00%	0.00%	0.00%
	Other	37	30	24	50.00%	34.09%	27.27%
Head Toss	Stand Interm.	57	41	25	16.52%	10.20%	6.22%
	Walk	15	17	5	4.35%	4.23%	1.24%
	Mew	6	4	5	1.74%	1.00%	1.24%
	Head Toss	112	250	113	32.46%	62.19%	28.11%
	Beg	52	0	135	15.07%	0.00%	33.58%
	Mounted	0	0	47	0.00%	0.00%	11.69%
	Other	103	90	72	29.86%	22.39%	17.91%
Respond to Beg	Stand Interm.	3	0	16	1.56%	0.00%	8.08%
	Walk	0	0	0	0.00%	0.00%	0.00%
	Mew	3	0	0	1.56%	0.00%	0.00%
	Head Toss	161	0	59	83.85%	0.00%	29.80%
	Beg	5	198	4	2.09%	100.00%	1.52%
	Mounted	0	0	93	0.00%	0.00%	46.97%
	Other	20	0	26	10.42%	0.00%	13.13%
Mount	Stand Interm.	1	0	N/A	0.68%	0.00%	N/A
	Walk	0	0	N/A	0.00%	0.00%	N/A
	Mew	0	0	N/A	0.00%	0.00%	N/A
	Head Toss	50	0	N/A	34.25%	0.00%	N/A
	Beg	94	0	N/A	64.38%	0.00%	N/A
	Mounted	0	147	N/A	0.00%	100.00%	N/A
	Other	1	0	N/A	0.68%	0.00%	N/A
Other	Stand Interm.	30	44	51	10.83%	13.50%	15.64%
	Walk	10	8	7	3.61%	2.45%	2.15%
	Mew	22	14	16	7.94%	4.29%	4.91%
	Head Toss	76	109	114	27.44%	33.44%	34.97%
	Beg	41	4	28	14.80%	1.23%	8.59%
	Mounted	0	0	3	0.00%	0.00%	0.92%
	Other	98	147	107	35.38%	45.09%	32.82%

Table 15. Common behavior occurrences following courtship and the first Mount for three stages of the mating season

Pre-Egg-Laying Stage[a] (23 May 2009)				Egg-Laying Stage[b] (6 June 2009)				Incubation Stage[c] (21-23 June 2009)			
Behavior	Male	Female	*p*[j]	Behavior	Male	Female	*p*[j]	Behavior	Male	Female	*p*[j]
Stand Interm.	43 (87.8%)	41 (83.7%)	0.83	Stand Interm.	51 (89.5%)	52 (91.2%)	0.92	Stand Interm.	37 (92.5%)	38 (95.0%)	0.91
Walk	18 (36.7%)	29 (59.2%)	0.11	Walk	40 (70.2%)	39 (68.4%)	0.91	Walk	23 (57.5%)	30 (75.0%)	0.34
Stand Preen	24 (49.0%)	36 (73.5%)	0.12	Stand Preen	29 (50.9%)	36 (63.2%)	0.39	Stand Preen	21 (52.5%)	27 (67.5%)	0.39
Shake Head	22 (44.9%)	12 (24.5%)	0.09	Shake Head	28 (49.1%)	25 (43.9%)	0.68	Shake Head	22 (55.0%)	23 (57.5%)	0.88
Look at Feet	11 (22.5%)	0 (0.0%)	0.0009	Look at Feet	20 (35.1%)	5 (8.8%)	0.003	Look at Feet	14 (35.0%)	8 (20.0%)	0.20
Shake Wings	2 (4.08%)	5 (10.2%)	0.26	Shake Wings	0 (0.0%)	23 (40.4%)	<0.0001	Shake Wings	2 (5.0%)	19 (47.5%)	0.0002
Stand Upright	13 (26.5%)	17 (34.7%)	0.47	Stand Upright	15 (26.3%)	16 (28.1%)	0.86	Stand Upright	10 (25.0%)	3 (7.50%)	0.052
Head Toss	6 (12.2%)[d]	10 (20.4%)[e]	0.44	Head Toss	12 (21.1%)[f]	19 (33.3%)[g]	0.21	Head Toss	6 (15.0%)[h]	7 (17.5%)[i]	0.78
Mount/Mounted	4 (8.2%)	4 (8.2%)	0.41	Mount/Mounted	5 (8.8%)	5 (8.8%)	0.76	Mount/Mounted	1 (2.5%)	1 (2.50%)	1.00
Choke	3 (6.2%)	2 (4.1%)	0.65	Choke	7 (12.3%)	6 (10.5%)	0.78	Choke	0 (0.0%)	0 (0%)	1.00

[a] 49 post-mount bouts.
[b] 57 post-mount bouts.
[c] 40 post-mount bouts.
[d] 2/6 = 33.3% of Head Toss with no subsequent Mounts.
[e] 6/10 = 54.5% of Head Toss with no subsequent Mounts.
[f] 8/12 = 66.7% of Head Toss with no subsequent Mounts.
[g] 14/19 = 73.7% of Head Toss with no subsequent Mounts.
[h] 5/6 = 83.3% of Head Toss with no subsequent Mounts.
[i] 6/7 = 85.7% of Head Toss with no subsequent Mounts.
[j] χ^2 expected values assume equal occurrences of each behavior between males and females; $df = 1$.

Table 16. Results of χ^2 tests comparing male and female post-Mount behavior occurrences by reproductive stage

	Male		Female	
Behavior	$\chi^{2\ a}$	*p*	$\chi^{2\ a}$	*p*
Stand Interm.	0.126	0.939	0.341	0.843
Walk	4.746	0.093	0.839	0.657
Stand Preen	0.081	0.960	0.633	0.729
Shake Head	0.497	0.780	5.931	0.052
Look at Feet	1.522	0.467	9.895	0.007[b]
Shake Wings	2.684	0.261	11.449	0.003[b]
Stand Upright	0.029	0.985	7.046	0.030[b]
Head Toss	1.121	0.571	2.552	0.279
Mount/Mounted	1.456	0.483	1.456	0.483
Choke	4.944	0.084	4.735	0.094

[a] $df = 2$; Expected values were based on the percentage that stage's observed post-Mount bouts made of the total number of post-Mount bouts observed (n = 147).
[b] Female Look at Feet, Shake Wings, and Stand Upright significant ($p < 0.05$).

Table 17. Mean pre- and post-Mount percent durations relative to pre- and post-Mount durations

Pre-first-Mount duration percentages

	Behavior	Stage[a]	Mean % of bout	*SD* (%)	*n*	*p*[b]
Male	Head Toss	PE	43.8%	34.1	44	
		E	42.5%	30.0	55	0.97
		I	44.5%	33.5	34	
	Resp. to Beg	PE	48.8%	27.7	38	
		E	47.3%	25.9	49	0.11
		I	59.4%	26.7	33	
	Stand Interm.	PE	13.0%	12.8	27	
		E	11.5%	8.3	26	0.52
		I	9.5%	10.1	12	
	Walk	PE	7.1%	8.6	16	
		E	8.5%	4.9	27	0.13
		I	7.1%	4.6	17	
	Mew	PE	7.8%	8.6	19	
		E	7.6%	8.1	12	0.77
		I	10.1%	9.3	15	
	Choke	PE	6.8%	5.9	9	
		E	9.2%	5.9	8	0.54
		I	7.6%	N/A	1	
	Long Call	PE	5.7%	3.2	6	
		E	5.5%	3.2	8	0.70
		I	5.6%	3.1	14	
Female	Head Toss	PE	47.9%	30.9	46	
		E	39.1%	25.6	54	0.42
		I	40.2%	29.7	36	
	Beg	PE	49.9%	27.1	38	
		E	47.5%	25.9	49	0.12
		I	59.5%	26.7	33	
	Stand Interm.	PE	8.6%	7.1	19	
		E	11.8%	9.0	32	0.33
		I	14.2%	12.2	11	
	Walk	PE	8.0%	6.4	17	
		E	12.4%	11.5	23	0.63
		I	12.5%	15.0	9	
	Mew	PE	5.8%	4.1	14	
		E	9.3%	4.9	9	0.13
		I	9.2%	10.7	5	
	Choke	PE	6.8%	5.9	9	
		E	10.8%	6.3	5	0.42
		I	7.6%	N/A	1	
	Long Call	PE	6.4%	3.0	5	
		E	6.0%	3.7	6	0.75
		I	3.2%	N/A	1	

Post-first-Mount duration percentages

	Behavior	Stage[a]	Mean % of bout	*SD* (%)	*n*	*p*[b]
Male	Stand Interm.	PE	56.8%	27.9	43	0.47
		E	50.4%	25.5	53	
		I	51.5%	29.0	35	
	Walk	PE	16.2%	12.1	18	0.53
		E	12.8%	10.1	40	
		I	14.3%	11.3	23	
	Stand Preen	PE	0.4%	29.4	13	0.70
		E	0.3%	27.1	17	
		I	0.3%	25.6	12	
	Shake Head	PE	7.0%	7.4	22	0.98
		E	6.0%	5.7	28	
		I	6.1%	4.9	22	
	Look at Feet	PE	18.3%	14.4	11	0.35
		E	16.0%	15.6	20	
		I	21.5%	14.2	13	
	Stand Upright	PE	22.5%	21.4	13	0.66
		E	13.4%	8.1	14	
		I	18.3%	17.6	9	
	Head Toss	PE	15.6%	10.6	5	0.77
		E	24.9%	23.9	12	
		I	22.9%	32.3	6	
Female	Stand Interm.	PE	55.1%	31.1	40	0.07
		E	38.5%	24.8	50	
		I	37.2%	23.5	39	
	Walk	PE	21.3%	25.8	29	0.89
		E	18.2%	14.6	38	
		I	18.1%	14.2	28	
	Stand Preen	PE	39.9%	23.1	16	0.53
		E	45.8%	25.8	27	
		I	37.9%	24.0	25	
	Shake Head	PE	5.1%	3.0	12	0.49
		E	4.5%	4.2	25	
		I	5.6%	4.9	23	
	Shake Wings	PE	5.7%	2.7	5	0.40
		E	7.7%	7.7	23	
		I	8.8%	5.6	19	
	Stand Upright	PE	26.9%	27.3	17	0.16
		E	11.4%	10.7	16	
		I	5.3%	2.6	2	
	Head Toss	PE	15.0%	11.6	9	0.32
		E	21.0%	23.8	19	
		I	29.2%	23.6	6	

[a] Stage of the mating season: PE = pre-egg-laying; E = egg-laying; I = incubation.
[b] Kruskall-Wallis test comparing ranks of the three breeding stages.

REFERENCE LIST

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Baird, P.H. (1990). Influence of abiotic factors and prey distribution on diet and reproductive success of three sea bird species in Alaska. – Ornis Scand. 21: 224-235.

Ball, G.F. & Balthazart, J. (2004). Hormonal regulation of brain circuits mediating male behavior in birds. – Physiol. Behav. 83: 329-346.

Ball, G.F. & Ketterson, E.D. (2008). Sex differences in the response to environmental cues regulating seasonal reproduction in birds. – Phil. Trans. R. Soc. B 363: 231-246.

Brown, R.G.B. 1967. Courtship behaviour in the lesser black-backed gull, *Larus fuscus*. – Behaviour 19: 122-153.

Burger, J. (1976). Daily and seasonal activity patterns in breeding laughing gulls. – Auk 93: 308-323.

Butler, R.G. & Janes-Butler, S. (1983). Sexual differences in the behavior of adult great black-backed gulls (*Larus marinus*) during the pre- and post-hatch periods. – Auk 100: 63-75.

Clayton, D.A. (1978). Socially facilitated behavior. – Q. Rev. Biol. 53: 373-392.

Erikstad, K.E., Fauchald, P., Tveraa, T., & Steen, H. (1998). On the cost of reproduction in long-lived birds: the influence of environmental variability. – Ecology 79: 1781-1788.

Fetterolf, P.M. & Dunham, D.W. (1985). Stimulation of courtship displays in ring-billed gulls using playback of vocalization. – Can. J. Zoolog. 63: 1017-1019.

Gochfeld, M. (1980). Mechanisms and adaptive value of reproductive synchrony in colonial seabirds. – In: Behavior of marine animals, Volume 4: Marine Birds (Burger, J., Olla, B.L, & Winn., H.E, eds). Plenum Press, New York, p. 207-271.

Good, T. P. (2002). Breeding success in the western gull x glaucous-winged gull complex: the influence of habitat and nest-site characteristics. – The Condor 104: 353-365.

Hailman, J.P. (1964). Breeding synchrony in the equatorial swallow-tailed gull. – Am. Nat. 76: 79-83.

Harris, M.P. (1970). Breeding ecology of the swallow-tailed gull, *Creagrus furcatus*. – Auk 87: 215-243.

Hayward, J.L., Galusha, J.G., & Henson, S.M. (2010). Foraging behavior of bald eagles at a marine bird colony and seal rookery in Washington. – J. Raptor. Res. 44:19-29.

Hayward, J.L. & Verbeek, N.A. (2008). Glaucous-winged gull (*Larus glaucescens*). – In: The Birds of North America Online (Poole, A., ed). Ithaca, NY: Cornell Laboratory of Ornithology; Retrieved from The Birds of North America Online: http://bna.birds.cornell.edu/bna/species/059

Henson, S.M., Dennis, B., Hayward, J.L., Cushing, J.M., & Galusha, J.G. (2007). Predicting the dynamics of field behavior in the field. – Anim. Behav. 74: 103-110.

Hosmer, D.W. & Lemeshow, S. (2000). Applied Logistic Regression. 2nd ed. – John Wiley and Sons, New York.

Kushlan, J.A. (1993). Colonial waterbirds as bioindicators of environmental change. – Colon. Waterbird. 16: 223-251.

The MathWorks. (2005). MATLAB/Statistics Toolbox. Version 7.1/Version 5.1. The MathWorks Inc., Natick, MA.

Moynihan, M. (1955). Some aspects of reproductive behavior in the black-headed gull (*Larus ridibundus ridibundus* L.) and related species. – Behaviour Suppl. 4, 1-365.

Moynihan, M. (1962). Hostile and sexual behavior patterns of South American and Pacific Laridae. – Behaviour Suppl. 8: 1-365.

Orzack, S.H. & Tuljapurkar, S. (2001). Reproductive effort in variable environments, or environmental variation *is* for the birds. – Ecology 82: 2659-2665.

Price, T., Kirkpatrick, M., & Arnold, S.J. (1988). Directional selection and the evolution of breeding date in birds. – Science 240: 789-799.

Salzer, D.W. & Larkin, G.J. (1990). Impact of courtship feeding on clutch and third-egg size in glaucous-winged gulls. – Anim. Behav. 39: 1149-1162.

Slagsvold, T. (1984). Clutch size variation in relation to nest predation: on the cost of reproduction. – J. Anim. Ecol. 53: 945-953.

Southern, W.E. (1974). Copulatory wing-flagging: a synchronizing stimulus for nesting ring-billed gulls. – Bird-Banding 45: 210-216.

Tasker, C.R. & Mills, J.A. (1981). A functional analysis of courtship feeding in the red-billed gull, *Larus novaehollandia scopulinus.* – Behaviour 77: 222-241.

Thomas, D.W., Blondel, J., Perret, P., Lambrechts, M.M., & Speakman, J.R. (2001). Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. – Science 291: 2598-2600.

Tinbergen, N. (1959). Comparative studies of the behaviour of gulls (*Laridae*): a progress report. – Behaviour 15: 1-70.

Tinbergen, N. (1960). The herring gull's world: a study of the social behavior of birds. – Harper & Row, New York. p. 103-124.

Vermeer, K. (1963). The breeding ecology of the glaucous-winged gull (*Larus glaucescens*) on Mandarte Island, B.C. – Occas. Pap. BC Prov. Mus. 13: p. 1–104.

Verbeek, N.A.M. (1986). Aspects of the breeding biology of an expanded population of glaucous-winged gulls in British Columbia. – J. Field Ornithol. 57: 22-33.

Visser, M.E., Both, C., & Lambrechts, M.M. (2004). Global climate change leads to mistimed avian reproduction. – Adv. Ecol. Res. 35: 89-108.

Weidmann, U. (1955). Some reproductive activities of the common gull, *Larus canus* L. – Ardea 43: 85-132.